

Figure 3

Average shell height versus time for size classes of *Lacuna vincta* in Magnolia, Massachusetts. The points are clustered into classes of a single presumed cohort; solid lines indicate average growth rates for these cohorts as determined by linear regression.

egg masses, juveniles, and adults were also observed on *Laminaria saccharina* blades washed up on the beach at Seal Harbor, Mt. Desert Island, Maine. On 2 November 1986, *Lacuna vincta* adults, juveniles, and egg masses were observed on *Chondrus crispus* at Perkins Cove in Ogunquit, Maine. *Lacuna vincta* egg masses were again observed at Ogunquit and Mt. Desert Island on 2 and 3 December 1986.

DISCUSSION

Our data show that spawning in *Lacuna vincta* is continuous, with year-round reproduction over a latitudinal range (42°30' in Magnolia, Massachusetts, to 44°30' in Mt. Desert Island, Maine) which is farther south than the sites in England and Ireland studied by SMITH (1973) and SOUTHGATE (1982). This finding is consistent with the observation of FRETTER & SHALE (1973) that *L. vincta* larvae are present in the water column off the coast of Plymouth, England, throughout the year, with veligers taken in hauls during every month of the year except three (February, June, and July).

These findings conflict with the suggestion of SOUTHGATE

(1982) that duration of a restricted spawning period may be directly related to latitude in *Lacuna vincta*. Regional differences in environmental features such as climate could possibly account for the difference between our findings on reproductive activity in North America and the findings of SMITH (1973) and SOUTHGATE (1982) in Great Britain. On the other hand, the assumption of SMITH (1973) and SOUTHGATE (1982) that *L. vincta* has a single annual spawning period may derive from the fact that they both restricted their studies to the littoral zone. THOMAS & PAGE (1983) report a sudden appearance of *L. vincta* in the littoral zone of New Brunswick, Canada, in June, and suggest that migration may occur from the sublittoral zone to the littoral zone at this time. SMITH (1973) reports similar findings in England, and during the winter months we have found adult *L. vincta* in sublittoral habitats when they were absent from littoral habitats. Studies of the life history of *L. vincta* should include the subtidal part of the population.

If intertidal subpopulations of *Lacuna vincta* in England experience immigrations from subtidal populations and/or more than one cohort per year, as observed in North America, then the life-history information provided by

SMITH (1973) and SOUTHGATE (1982) may be inaccurate. Both studies calculate mortality based on the assumption of a closed intertidal population comprised of a single cohort in each year.

Regression and ANCOVA indicate that the two distinct size classes observed for 18 of 20 monthly samples of the *Lacuna vincta* population at Magnolia are representatives of different sets of individuals that recruited at the same time (which we refer to as cohorts). Regressed against time, monthly mean shell heights ascend through the same range of values, as would be expected if size classes are actually cohorts growing over time. ANCOVA shows that the size classes followed through time all grow at the same rate, as would be expected for different cohorts of a given population. Four of the five cohorts seen were initiated during our study, one each for the months of August, September, October, and January. Because egg masses were observed year round, this indicates that reproduction was occurring in Magnolia throughout the year, but that recruitment occurred in pulses.

The causes of variable recruitment of marine invertebrates are still poorly known, but two components are believed to be involved: (1) variation in reproductive output and (2) variation in mortality and distribution of larvae while in the water column (GAINES & ROUGHGARDEN, 1987). In Popplestone Cove, the occurrence of five distinct cohorts over 25 months of continuous reproduction indicates pulsed recruitment to this subtidal *Lacuna vincta* population similar to the pulsed recruitment seen to limit density in some intertidal populations (PAINE, 1977; SUTHERLAND & ORTEGA, 1986; GAINES & ROUGHGARDEN, 1987). Because *L. vincta* has continuous reproductive output, the pulsed recruitment observed in this subtidal population is likely to be the result of temporal variation of either events of transport into Popplestone Cove or larval mortality. Further field work on organisms like *L. vincta* is needed to identify the environmental factors that produce pulsed recruitment in subtidal populations, and to determine the importance of these factors to population regulation.

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Recruitment of the Estuarine Soft-Bottom Bivalve *Polymesoda caroliniana* and Its Influence on the Vertical Distribution of Adults

by

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Abstract. In the Sopchoppy-Ochlockonee estuary of northern Florida, adults of the infaunal corbiculacean bivalve *Polymesoda caroliniana* occur in the intertidal zone and, rarely, subtidally. Examinations of the distribution of juveniles and the pattern of recruitment into defaunated sediments indicate that vertical zonation in *P. caroliniana* is determined either at settlement or very shortly after settlement. Reciprocal transplants of subtidal and intertidal sediments, as well as manipulations of presence or absence of adult *P. caroliniana* suggest that *P. caroliniana* larvae settled selectively at intertidal elevations and actively selected an intertidal substratum.

INTRODUCTION

Vertical zonation of benthic organisms is an easily observed phenomenon in marine intertidal areas that has been explained as resulting from interactions of physical and biological factors with the dispersal patterns and survival rates of benthic organisms (see reviews by DAYTON, 1984; UNDERWOOD & DENLEY, 1984). Although CONNELL (1972) generalized that physical factors control upper distributional limits and biological factors control lower bounds, zonation is a complex and often site-specific event that is not easily interpreted (UNDERWOOD & DENLEY, 1984; ROUGHGARDEN *et al.*, 1988). There have been numerous studies of vertical zonation and boundary phenomena on rocky shores (*e.g.*, CONNELL, 1961a, b, 1972; FRANK, 1965; PAINE, 1966, 1974; DAYTON, 1971; MENGE, 1976), but similar studies concerning soft-bottom intertidal areas are comparatively uncommon (WOODIN, 1974, 1976; VIRNSTEIN, 1977; PETERSON & ANDRE, 1980; DAYTON, 1984), primarily because of the inherent difficulties in censusing and experimentally manipulating the generally small or mobile infauna (DAYTON & OLIVER, 1980). Most of the research on soft-bottom intertidal macro-invertebrates has basically concurred with the classic notion of CONNELL (1972) that physical factors limit upper bounds and biological factors control lower bounds (DEXTER, 1969; GREEN & HOBSON, 1970; HOLLAND & POLGAR, 1976; HOLLAND & DEAN, 1977). However, GREEN (1968) suggested that a lack of adequate feeding time can preclude

organisms from intertidal regions, and WOODIN (1974) demonstrated that both biological and physical factors were involved in the control of some intertidal polychaete distributions, but added that physical factors should be more important intertidally. Because of the paucity of rigorous manipulative studies and the general lack of data, it is unclear how the principles of intertidal zonation, developed from studies of rocky intertidal habitats, apply to soft-bottom habitats.

A current focus of research is the role of larvae in determining the vertical zonation of marine benthic invertebrates. In order to assess the effects of physical and biological factors on vertical distribution, the significance of larval dispersal in the nearshore environment and settlement in the intertidal habitat must be understood (CONNELL, 1985; ROUGHGARDEN *et al.*, 1988). Unfortunately the planktonic phase remains unknown for the vast majority of species (CONNELL, 1985). In the absence of data on settlement, information on recruitment (*sensu* BUTLER & KEOUGH, 1981; KEOUGH & DOWNES, 1982) can be useful, if carefully interpreted (but see cautions by HADFIELD, 1986; WOODIN, 1986). Available data indicate that many larvae settle non-randomly (MEADOWS & CAMPBELL, 1972; CRISP, 1974; STRATHMANN *et al.*, 1981; GROSBERG, 1982; HANNAN, 1984; BUTMAN *et al.*, 1988), and that the vertical range of adults may be further narrowed (CONNELL, 1961a, b; DAYTON, 1971; STRATHMANN & BRANSCOMB, 1979) suggesting that both settlement and

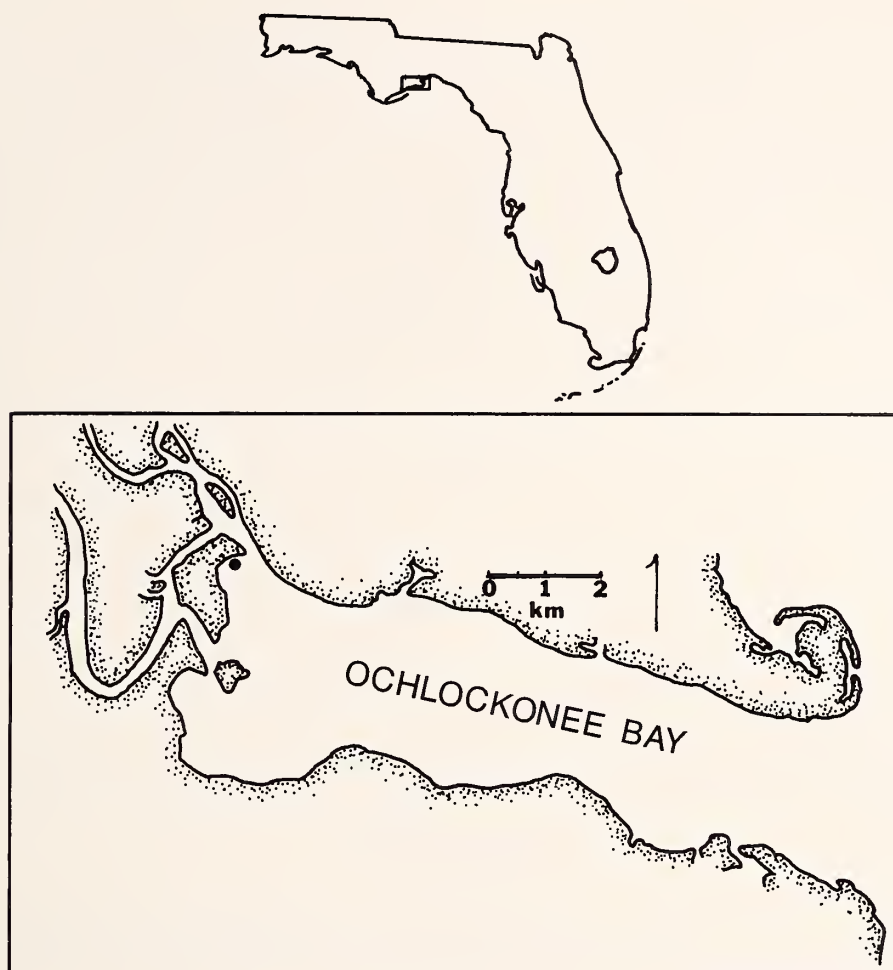


Figure 1

Map of Florida. Inset shows Ochlockonee Bay ($29^{\circ}58'N$, $84^{\circ}25'W$); ● indicates location of study site.

post-settlement events are important. It is unclear for most species whether active habitat selection, passive deposition, or a combination of passive and active modes are involved (BUTMAN, 1987).

In this paper, I document the vertical distributions of adults and recruits of the corbiculacean bivalve *Polymesoda caroliniana* (Bosc, 1801) in a north Florida estuary, document that the vertical distribution of adults is identical to that of recruits, and discuss ways in which this pattern may arise.

MATERIALS AND METHODS

Study Site

Surveys and experiments were performed in the oligohaline portion of the Sopchoppy-Ochlockonee estuary of northern Florida (Figure 1). This shallow, turbid, and well-mixed estuary is typical of many estuaries fringing the Gulf of Mexico. The estuary is bordered by an exten-

sive stand of *Juncus roemerianus* between the elevations 0 and +1.0 m. Elevations for the study area, determined by surveying tidal levels in relationship to a USCGS benchmark, are reported as deviations from MLLW (mean lower low water). The tidal range in the vicinity of the study site is approximately 1.2 m (OLSEN, 1973).

Adult Distribution

Preliminary surveys indicated that hand-collected samples were necessary to accurately assess adult (clams greater than 20 mm in length [OLSEN, 1976]) distributions. A rectangular 18×27 m plot was delineated in the field. The shoreward edge of this rectangle was a line, parallel to the shoreline, located at an elevation of +1.0 m. The seaward edge of the rectangle was located at an elevation of -0.5 m. This rectangle was subdivided into six laterally placed blocks, with nine vertical strata in each block. Vertical strata are defined as areas of bottom at different

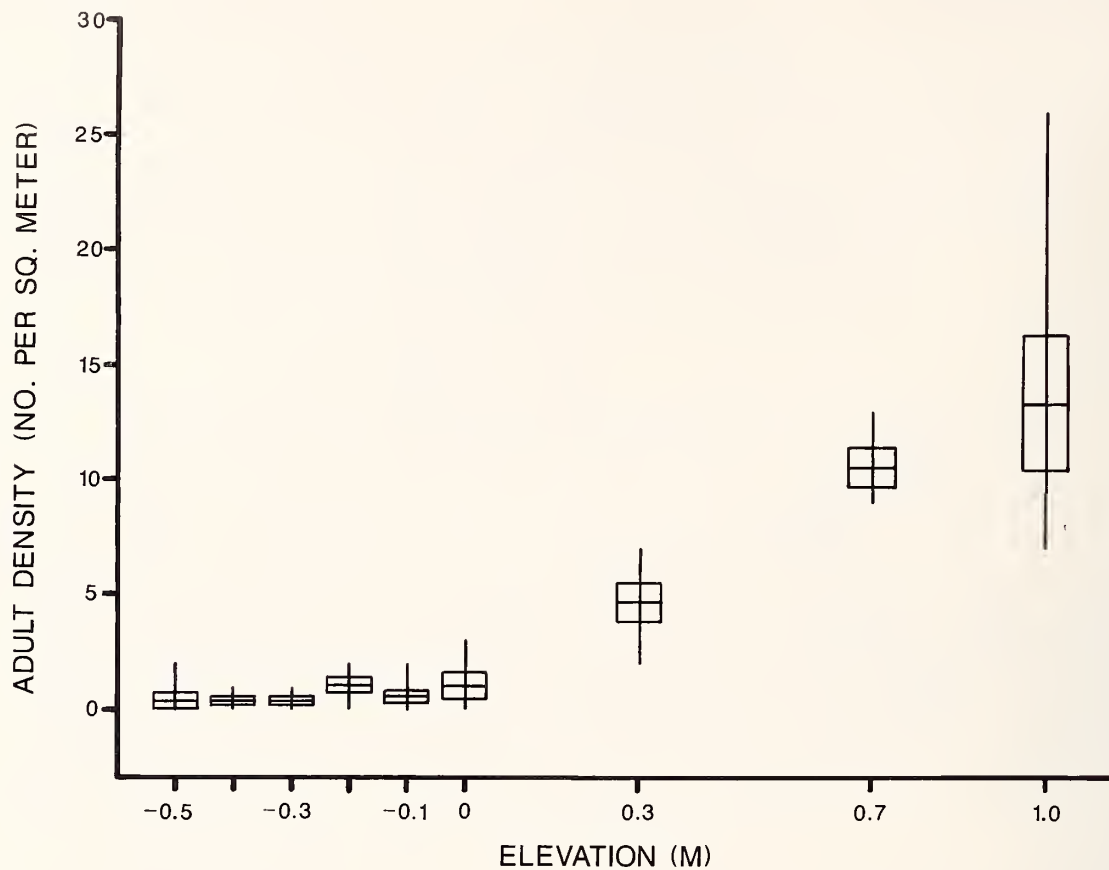


Figure 2

Abundance of adult *Polymesoda caroliniana* by elevation at the study site in Ochlockonee Bay. Data from all sampling dates are included. Figures display range, mean, and $\pm 1SE$.

elevations. Beginning in September 1982, one block from each stratum was selected randomly for sampling. Samples were collected every two months for one year and no block was sampled more than once. Because adult and juvenile surveys were designed for randomized block analysis, only one observation per cell was taken. This is not an unintentional lack of replication, and in any case the survey data are presented in this paper simply to demonstrate the pattern of vertical distribution shown by adult and juvenile stages. All clams were removed from a 1-m² quadrat placed randomly within the 3 × 3 m stratum-by-block sampling cells selected for a particular sampling date. Clams removed from these quadrats were labeled according to collection location, counted, and preserved, and their linear dimensions were measured. At the conclusion of the sampling period, all 54 stratum-by-block combinations had been sampled.

Juvenile Distribution

Because the adult survey disturbed large areas of the bottom, I sampled for recruits and small juveniles (clams

Table 1

Polymesoda caroliniana. Abundance and distribution of juveniles from upper Ochlockonee Bay study site, 1982–1983. Numbers at each elevation and date are numbers per m².

Elevation (m)	Date					
	Sep-82	Nov-82	Jan-83	Mar-83	May-83	Jul-83
+1.0	230.8	57.7	365.4	500.0	307.7	557.7
+0.7	653.8	1942.3	1230.7	173.1	2403.8	519.2
+0.3	76.9	19.2	19.2	38.5	38.5	38.5
0	57.7	0	0	19.2	0	19.2
-0.1	0	19.2	0	0	0	0
-0.2	19.2	0	0	0	0	0
-0.3	0	0	0	0	0	0
-0.4	0	0	0	0	0	0
-0.5	0	19.2	0	0	0	0

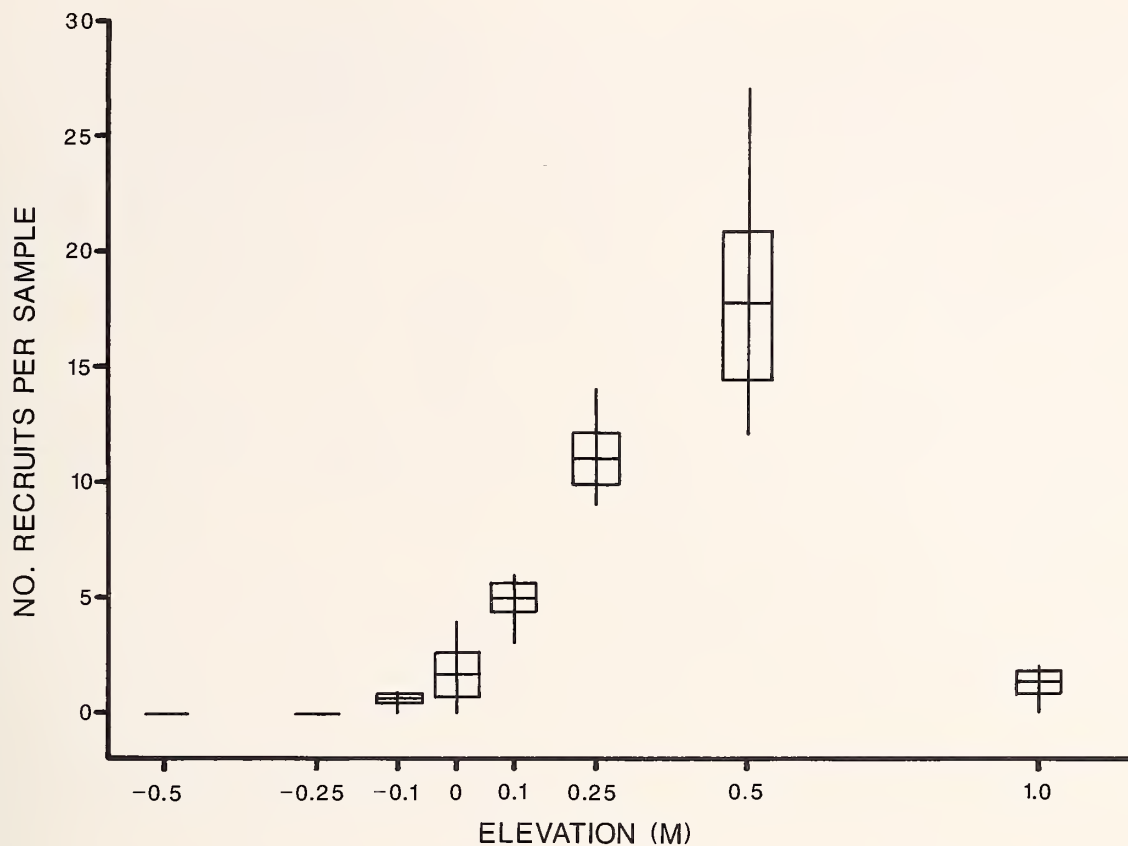


Figure 3

Abundance of *Polymesoda caroliniana* recruits to defaunated cores along a vertical gradient in upper Ochlockonee Bay, September to October 1982. Figures display range, mean, and ± 1 SE.

less than 1 yr old and less than 20 mm in length) of *Polymesoda caroliniana* in an adjacent plot. The juvenile survey area was identical in dimension and elevation to the adult survey area. Again, there were 54 stratum-by-block combinations. Each of the nine vertical strata was sampled every two months, and only one block per stratum was sampled on each date. No block-by-stratum combination was sampled more than once. Beginning in September 1982, one randomly located grab sample was taken from each of the nine randomly selected sample cells for that sample date. Samples were collected using a modified large Ekman grab (WILDCO® 197-G10, area of bite 0.052 m²) and were washed on a 500- μ m sieve. Materials retained were preserved, and bivalves were subsequently sorted and counted.

Distribution of Recruits

An additional transect extending between the elevations +1.0 to -0.5 m, and perpendicular to the shoreline, was established near the survey site in September 1982. Cores of surface area 0.014 m², and 1 L in volume, were taken in triplicate at the following elevations: +1.0 m, +0.5 m,

+0.25 m, +0.1 m, 0.0 m, -0.1 m, -0.25 m, and -0.5 m. These elevations were roughly equivalent to the elevations of the strata used in the adult and juvenile surveys. Cores were placed in 1-L polypropylene beakers, defaunated by freezing, and returned to the experimental site at the same elevations from which they were removed. After 1 month, the cores were retrieved and all *Polymesoda caroliniana* recruits counted. This experiment was performed in September because this was a time of heavy settlement (pers. obs.).

Recruit Selectivity

To determine if larvae were settling selectively based on elevation or origin of substrate, an experiment was conducted in December 1982 (when, once again I observed settlement to be dense). Twelve cores (surface area 0.014 m², volume 1 L) were collected from the study site at each of two tidal elevations, +0.25 m and -0.25 m, and defaunated by freezing. Twelve adult *Polymesoda caroliniana* were collected and one adult was placed in each of six intertidal cores and six from the subtidal elevation. Three replicates of each of the following combinations were placed

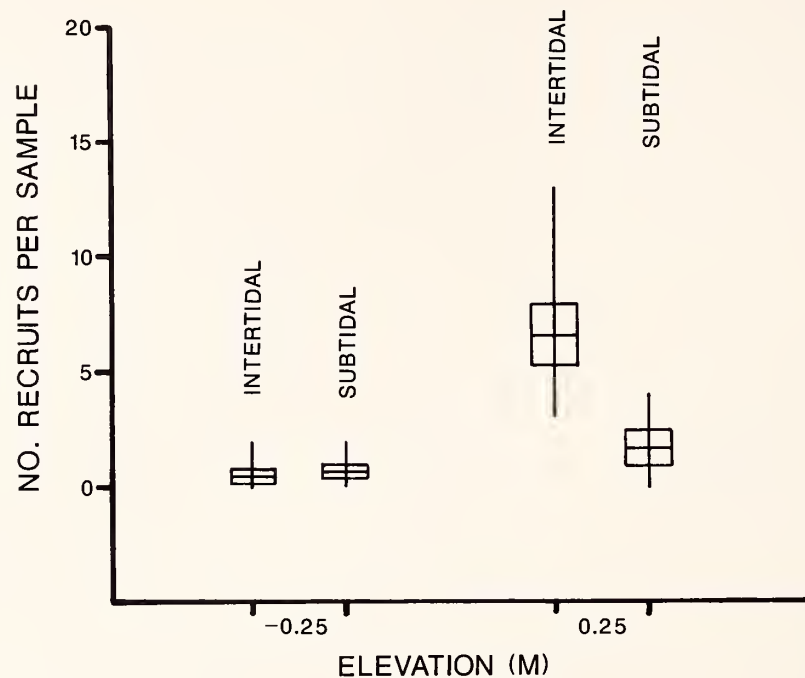


Figure 4

Recruitment of *Polymesoda caroliniana* to defaunated cores at tidal elevations +0.25 m and -0.25 m, December 1982 to January 1983. Each elevation had replicates of sediment of both intertidal and subtidal origin. Figures display range, mean, and ± 1 SE.

at the elevations +0.25 and -0.25 m: intertidal sediments alone, intertidal sediments with one adult *P. caroliniana*, subtidal sediments alone, and subtidal sediments with one *P. caroliniana*. The sediment level in each core was flush with the surrounding substratum. After 1 month the cores were retrieved, and all *P. caroliniana* recruits were counted.

Voucher Specimens

Specimens of *Polymesoda caroliniana* collected in the course of this research have been deposited in the Florida Department of Natural Resources Invertebrate Collection, lot number FSBCI 37174.

RESULTS

Adult Distribution

Across all sampling dates nearly 90% of adult *Polymesoda caroliniana* collected were found to occur intertidally (Figure 2). The greatest abundance was in the highest stratum, +1.0 m, and only occasionally were adults collected subtidally.

Juvenile Distribution

Juvenile *Polymesoda caroliniana* were collected almost exclusively from intertidal elevations (Table 1). Ninety-eight percent of the juveniles collected in the course of this

study occurred at intertidal elevations, with the greatest concentration at the +0.7 m elevation. Juveniles were rare below MLLW.

Distribution of Recruits

Ninety-four percent of the *Polymesoda caroliniana* recruitment into defaunated sediments occurred at intertidal elevations, with the greatest concentration at +0.5 m (Figure 3). Recruitment to subtidal elevations was extremely rare. These data indicate that recruitment occurs across a vertical range nearly identical to that of the juvenile and adult stages.

Recruit Selectivity

Polymesoda caroliniana recruited predominately to intertidal elevations (87% of all recruits; Figure 4), confirming results of the previous recruitment experiment. The data suggest that *P. caroliniana* recruits more heavily to intertidal sediment in preference to subtidal sediment when both are located at the same elevation. The results further suggest that larvae will not settle in the subtidal, even into sediment of intertidal origin. Recruitment data were analyzed utilizing a two-way completely randomized ANOVA. Although there were 24 experimental chambers, data from the subtidal chambers were eliminated; virtually no recruitment occurred subtidally, and the large number of

Table 2
Analysis of variance for effects of sediment type and presence or absence of conspecific adults on recruitment of *Polymesoda caroliniana*.

Source	d.f.	SS	MS	F	P-value
Sediment type	1	70.08	70.08	7.19	0.05 > P > 0.025
Adult presence/absence	1	0.75	0.75	0.077	P > 0.25
Sediment type by adult presence/absence	1	0.08	0.08	0.008	P > 0.25
Residual	8	78.00	9.75		
Total	11	148.92			

zeroes violates the assumption of normality of residuals underlying the *F*-test. Sediment type had a strong effect on the recruitment of *P. caroliniana* juveniles ($0.025 < P < 0.05$), but the presence of adult *P. caroliniana* had no detectable effect (Table 2).

DISCUSSION

The present experiments indicate that *Polymesoda caroliniana* recruited primarily to the intertidal and shallow subtidal areas of the study site, a pattern that is reflected in the vertical distributional pattern of juvenile and adult *P. caroliniana*. The concordant patterns of recruit, juvenile, and adult vertical distributions imply that larval settlement preferences play a key role in casting the distributions of post-settlement stages. This conclusion is further supported by the results of the substratum transplant experiments. Nevertheless, because larval settlement was not directly observed it remains possible that elevation-specific differences in early post-settlement mortality play some role in casting the distributions of post-settlement individuals. *Polymesoda caroliniana* larvae could settle preferentially in the vertical range occupied by adult clams. Larvae may be induced to settle in response to cues from specific substrata, microbial faunas, conspecifics, or specific flora (KNIGHT-JONES, 1953; WILLIAMS, 1964; BAYNE, 1969; KNIGHT-JONES *et al.*, 1971; MEADOWS & CAMPBELL, 1972; CRISP, 1974; KECK *et al.*, 1974; CAMERON & SCHROETER, 1980; STRATHMANN *et al.*, 1981; HIGHSMITH, 1982; HUI & MOYSE, 1982; SCHMIDT, 1982). Larvae may also recruit passively through active selection of vertical position in onshore moving water masses (FORWARD, 1976; GROSBURG, 1982; GAINES *et al.*, 1985). Finally, larvae may act as passive particles during settlement, being deposited on the substratum at sites where particles with fall velocities similar to larvae initially settle (HANNAN, 1984; BUTMAN, 1987; BUTMAN *et al.* 1988). It is not known, however, what mechanisms are involved in the pre-settlement distribution and actual settlement of *P. caroliniana* larvae.

Results of the present research suggest that *Polymesoda caroliniana* larvae, when offered a choice in the field, settle preferentially on intertidal sediments rather than subtidal sediments. However, *P. caroliniana* larvae were not induced into settling subtidally into intertidal sediment plots as

STRATHMANN *et al.* (1981) were able to induce *Balanus glandula* to settle on sub-optimal lower substrata. Settlement and recruitment patterns can be quite different because of post-settlement effects (CAFFEY, 1985; CONNELL, 1985; KEOUGH & DOWNES, 1986), but because I observed virtually no subtidal recruitment, settlement is probably rare subtidally unless mortality is rapid and high compared to that at intertidal levels. Results of my work suggest that recruitment reflects settlement in the *P. caroliniana* population that I studied, and by inference that settlement is probably the determining factor in the vertical distribution of adults.

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